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Marine migration and habitat use of anadromous brown trout (*Salmo trutta*)

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Abstract: The biology and ecology of anadromous brown trout (*Salmo trutta*) at sea is poorly understood. This study provided information on spatial and temporal distribution of sea trout in the ocean. The behaviour of 115 individuals (veteran migrants, 270–700 mm) was tracked by using acoustic telemetry in a fjord system during April–September in 2012–2013. Overall, fish spent 68% of their marine residence time close to river mouths (<4 km). Most fish registrations (75%) were in nearshore habitats, but pelagic areas were also used. The maximum migration distance of tagged fish was categorized as short (<4 km from river mouth, 40% of fish), medium (4 – ~13 km, 18% of fish), or long (>~13 km, 42% of fish). Long-distance migrants had poorer body condition in spring prior to migration, used pelagic areas more often, and returned earlier to fresh water than short- and medium-distance migrants. Marine residence time was 7–183 days and was positively correlated to body length and smolt age, but negatively correlated to the date of sea entry.

Résumé : La biologie et l'écologie de la truite de mer anadrome (*Salmo trutta*) en mer ne sont pas bien comprises. Cette étude présente de l'information sur la répartition spatiale et temporelle des truites de mer dans l'océan. Le comportement de 115 individus (des migrateurs vétérans, 270–700 mm) a été suivi par télémétrie acoustique dans un réseau de fjords, d'avril à septembre, en 2012–2013. Dans l'ensemble, les poissons passaient 68 % de leur temps de résidence en mer près d'embouchures de rivières (<4 km). Si la plupart des observations (75 %) étaient dans des habitats côtiers, des zones pélagiques étaient également utilisées. La distance de migration maximum des poissons marqués a été classée selon qu'elle était courte (<4 km de l'embouchure d'une rivière, 40 % des poissons), intermédiaire (de 4 à ~13 km, 18 % des poissons) ou longue (>~13 km, 42 % des poissons). Les individus migrant sur de longues distances présentaient un moins bon embonpoint au printemps avant la migration, utilisaient plus souvent des zones pélagiques et retournaient plus tôt en eau douce que les individus migrant sur des distances intermédiaires et courtes. Les temps de résidence en mer allaient de 7 à 183 jours et étaient positivement corrélés à la longueur du corps et à l'âge à la smoltification, mais négativement corrélés à la date de l'entrée en mer. [Traduit par la Rédaction]

Introduction

The brown trout (*Salmo trutta*) is an iteroparous salmonid species with indigenous populations in Europe, North Africa, and western Asia (MacCrimmon et al. 1970). It has been introduced by humans to all other continents except Antarctica (MacCrimmon and Marshall 1968). The brown trout is an opportunistic carnivore that, with its large ecological variability, has adapted to and found suitable niches in a variety of habitat types (Klemetsen et al. 2003). Brown trout often migrate to utilize the best suited habitat during different stages of its life cycle, moving either within freshwater systems or repeatedly between freshwater and marine habitats, to ultimately increase their individual fitness (Jonsson and Jonsson 1993). By exploiting better feeding habitats (i.e., the sea or a lake), migration can enable individuals to attain higher growth rates, larger sizes-at-age, and for females higher fecundities (Hendry et al. 2004), all of which may provide fitness benefits. The costs related to migration may include physiological adjustments, the allocation of energy for swimming, and increased probability of mortality (e.g., owing to predation, parasitism, and diseases during migration; Gross et al. 1988; Jonsson and Jonsson 1993).

Brown trout populations in coastal rivers may consist of both anadromous (hereinafter referred to as sea trout) and resident individuals originating from the same parents (Jonsson and Jonsson 1993). The mechanisms controlling whether an individual becomes resident or migratory are yet to be fully understood (Acolas et al. 2012), but an individual's tendency to migrate seems partly genetically determined and partly caused by phenotypic plasticity (Jonsson and Jonsson 1993). Factors such as metabolic rate, growth rate, body size, energy reserves, sex, and genetics are thought to influence whether an individual adopts migratory or resident behaviour (Thorpe 1987; Forseth et al. 1999; Wysujack et al. 2009). The balance between migration and residency is influenced by environmental factors such as food availability, fish density, and interspecific competition in combination with inter-individual differences, presumably underpinned by genetically determined reaction norms (Pulido 2011). Similar intrinsic and environmental factors may also influence individual behavioural

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strategies during marine migrations, determining whether to become a short- or long-distance migrant and which feeding habitats to utilize. However, little is known about the interindividual variation of migration behaviour and strategies in the marine environment and of the factors that may influence this variation.

Previous studies of sea trout in the marine environment have revealed a large variation in migration timing, residence periods (Jensen 1968; Jonsson 1985; Jensen and Rikardsen 2008; Jensen et al. 2012), migration distance (Berg and Berg 1987; Jensen et al. 2014), and prey choice (Knutsen et al. 2001; Rikardsen and Amundsen 2005; Rikardsen et al. 2007). In Europe, sea trout can enter estuaries from fresh water during all months of the year (Went 1962; Jonsson and Jonsson 2002, 2009), and the marine residence time may differ considerably among individual fish. For instance in Irish rivers, marine residence time was found to vary between 43 and 362 days (Piggins 1964). Migratory distances may also differ significantly. In Russia, Chernitsky et al. (1995) suggested that some trout resided in the estuary of the River Varsina, while others migrated to the open Barents Sea. Intrapopulation variation in marine migration distance was also recorded in a Danish population, where 47% of the tagged sea trout postsmolts remained close to their home river in a coastal fjord, and 53% migrated to the open Kattegat Sea (del Villar-Guerra et al. 2014). The authors suggested that the variation in migration distance was consistent with a continuum of partial migration, in which a decision-making point existed after fjord entry on whether to stay in the fjord or migrate to the open sea. However, both smolts and sea trout kelts (repeat spawning individuals) in a nearby fjord all migrated into the Kattegat Sea (Aarestrup et al. 2014, in press), demonstrating a large life history variability both within and among nearby populations.

During the last decades, the abundance of sea trout has declined markedly in many regions (ICES 2013). As an example, the catches in Norwegian rivers have, except for the northernmost areas, declined by 23%–66% during the last two decades (Anonymous 2011). Recent findings from several other countries where sea trout occur indicate similar decreases, and for some areas it is hypothesized that this results from reduced marine survival caused at least in part by changes in food supply or increased parasite infestations related to fish farming (ICES 2013). In sea trout populations, mortality in the freshwater phase, especially during the earliest embryonic and postemergence life stages, can have a population regulating effect, whereas mortality in the marine phase is not regulatory, but has a population reducing effect (Milner et al. 2003; Jonsson and Jonsson 2011). Hence, it is not believed that there are compensatory mechanisms for additional mortality in the marine phase, and elevated marine mortality rates can result in a proportional reduction in the number of spawning adults. Because sea trout typically are females (e.g., Knutsen et al. 2004; Jensen et al. 2012), additional marine mortality has an accentuated potential to negatively affect population recruitment by reducing the egg supply. The marine phase is therefore an important life stage of sea trout. However, their biology and ecology in the sea is poorly understood (Drenner et al. 2012; ICES 2013), and to understand the causes for the decrease in the abundance of sea trout in many regions, increased knowledge on the marine life stage is fundamental. To identify which anthropogenic or natural factors impact sea trout and to what extent, it is essential to determine the habitats utilized by the sea trout at different times. Migration distance is also important, as short-distance migrants will mainly be impacted by local factors close to a population's river mouth, whereas long-distance migrants may be impacted by multiple factors acting along the migration routes and in the different feeding habitats.

Most previous marine tracking studies of sea trout have focused on postsmolt migration behaviour (e.g., Moore et al. 1998; Thorstad et al. 2004), whereas only a few studies have covered older life stages (Bendall et al. 2005; Jensen and Rikardsen 2008, 2012; Jensen et al. 2014; Aarestrup et al., in press). The aim of the present study was to provide novel information on the marine habitat utilization during the summer season for sea trout that had previously performed one or more previous marine migrations, termed veteran migrants. Spatial and temporal distributions of tagged fish were recorded throughout the summer using acoustic telemetry in a marine fjord in Central Norway. Specifically, marine migration distance from the trout's putative home river mouth, marine residence time, and utilization of littoral versus pelagic habitat were examined. To explain individual variation in marine residence time and possible differences among the short-, medium-, and long-distance migrants, information on individual morphometric (body length, body condition, age) and life history characteristics (back-calculated smolt length, age at smolting, previous number of marine seasons) were analysed in relation to the observed migration patterns.

Materials and methods

Study area

The study was performed in two interconnected fjords (Hemnfjord and Snillfjord) in Sør-Trøndelag County, Central Norway. Together, the two fjords cover more than 60 km^2 of sea surface and have 65 km of shoreline (Fig. 1). The fjord system is connected to the open sea through a 36 km long strait.

The Søa watercourse has a drainage basin of 113 km^2 and a mean annual water discharge of 13.9 m^3·s^{-1}. The freshwater section accessible to anadromous fish is 10.2 km long and includes Lake Rovatnet (surface area 7.65 km^2), which offers suitable overwintering habitat and conditions for sea trout. River Søa drains from the lake to the sea in Hemnfjord.

The River Snilldalselva consists of two branches, Snilldalselva and Bergselva. Snilldalselva has a drainage basin of 42.7 km^2, mean annual water discharge of 1.4 m^3·s^{-1}, and a 4.8 km long section accessible to anadromous trout. Bergselva has a drainage basin of 69.3 km^2, mean annual water discharge of 2.1 m^3·s^{-1}, and an accessible stretch of 1.1 km. Both branches are highly influenced by floods and have few deep pools; consequently, they are considered to be poor overwintering areas for sea trout.

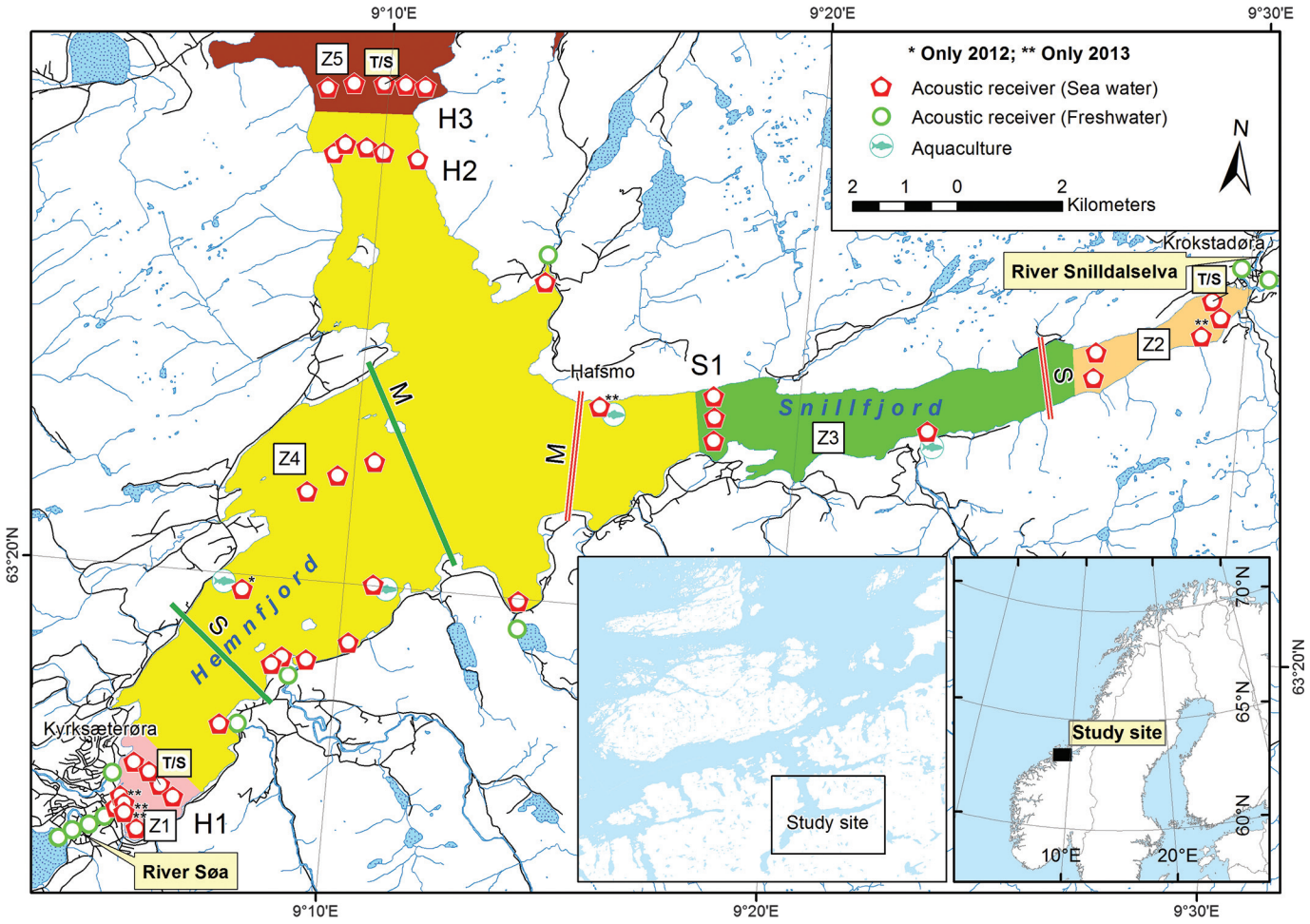
Environmental variables

Three temperature and salinity recorders (DST milli-CT, StarOddi Ltd., Iceland) were deployed in the fjord system, the first 1 km from the mouth of the River Søa in the inner Hemnfjord (Array H1; Fig. 1), a second 600 m from the river mouth of the River Snilldalselva in the inner Snillfjord (Fig. 1), and the third at the middle receiver of the outermost array (Array H3; Fig. 1). They were mounted at 1 m depth on the same moorings as the automatic acoustic receivers.

Fish capture and tagging

Five groups of sea trout were captured and tagged with acoustic transmitters during 12 April 2012 – 12 May 2013 (Table 1). A total of 80 individuals were tagged in the Søa watercourse, consisting of 30 fish tagged in the outlet of Lake Rovatnet during the spring of 2012 (HS12 tagging group), 21 fish tagged in Lake Rovatnet during autumn 2012 (HA12), and 29 fish tagged in the river mouth of River Søa during the spring of 2013 (HS13). A total of 35 individuals were tagged in River Snilldalselva, consisting of 20 fish tagged during autumn 2012 (SA12) and 15 fish tagged during spring 2013 (SS13). The fish were captured using three to five gillnets with 35–42 mm mesh width. The nets were checked continuously, and captured fish were retrieved as soon as vibrations or visual observations indicated a fish was entangled. This reduced fish stress and injuries. The fish were taken out of the nets by cutting net mesh with scissors to prevent damage to gills, skin, and scales. Prior to tagging, the captured fish were kept up to 2 h in a net cage in a calm part of the river or shoreline.

Fig. 1. Locations of automatic receivers (red pentagons = marine; green circles = fresh water) and temperature and salinity data loggers (T/S) in the study area. Area zones (Z1–Z5) and outer boundaries for definition of short (S) and medium (M) migration distance (fish from the Søa watercourse = green lines; fish from the Snilldalselva River = red lines). Arrays across the fjord included both nearshore and pelagic receivers (H1, H2, H3, and S1).



The sea trout were implanted with individually coded acoustic transmitters. Study partners contributed tags to the study, which resulted in using different models of tags having different characteristics and capabilities depending on partner resources and research interests. The different models had the same shape but differed in length and diameter, which allowed adaptation of tag size to the length of the fish (HS12: $n = 15$ model MP-9-long, natural length (L_N) 335–440 mm; $n = 15$ model MP-13, L_N 350–600 mm; HA12: $n = 10$ model V9-2x, L_N 270–380 mm; $n = 11$ model V13-1x, L_N 370–700 mm; SA12: $n = 5$ model MP-9-long, L_N 310–400 mm; $n = 6$ model MP-13, L_N 340–650 mm; $n = 9$ model V13-1x, L_N 340–440 mm; HS13: $n = 29$ model ADT-9-long, L_N 330–580 mm; SS13: $n = 15$ model ADT-9-long, L_N 320–460 mm). Natural length of the fish was measured from the tip of the snout to the tip of the longer lobe of the caudal fin, without compressing the lobes along the midline. Estimated battery life was 246 days (MP-9-Long), 267 days (ADT-9-long), 282 days (V9-2L), 525 days (MP-13), and 622 days (V13-1L). Hence, 41 fish tagged in 2012 could also be tracked in 2013. Transmitter models MP and ADT were produced by Thelmabiotel AS, Norway, and all V models by VEMCO Inc., Canada. Tag size was chosen according to body length and condition of the fish to minimize tag size relative to fish size. Tag mass in air relative to fish body mass was on average 1.46% (range 0.30%–3.09%). The tag used for any individual fish was believed to be small enough that it would not substantially affect behaviour or survival (e.g., Cooke et al. 2011).

Prior to tagging, the fish were anaesthetized with 2-phenoxyethanol (EC No. 204-589-7; SIGMA Chemical Co., USA; 0.5 mL·L^{-1} water). A 1.5–2 cm incision was made in the body cavity on the ventral surface anterior to the pelvic girdle. After the tag was inserted via the incision into the body cavity, the incision was closed using two independent monofilament sutures (RESORBA Wundversorgung GmbH & Co. KG, Germany; 5/0 Resolon). During the 3–5 min surgery, the gills were gently irrigated. After surgery, the fish were placed in a holding tank for recovery (3–5 min) before they were released in a calm part of the river or near the shoreline close to the capture site.

Tracking of tagged fish

The tagged fish were tracked using a total of 50 acoustic receivers (Vemco Inc., Canada, models VR2W and VR2). Of these, 39 were deployed in the fjord system, while 11 were deployed in different watercourses, including those where the fish were captured for tagging (Fig. 1). All receivers deployed in the fjord were mounted on moorings 5 m below the surface and were operative from 20 April 2012 – 4 December 2013. The receivers deployed in rivers were moored on 50 mm iron pipes, which were hammered into the riverbed. With exception of the four receivers in River Søa between Lake Rovatnet and the Hemnfjord, which were in operation during the whole study period, all receivers in freshwater habitats were operative from 20 April 2012 to 2 December 2012 and from 22 April 2013 to 4 December 2013.

Table 1. Tagging groups, tagging location, number of individuals, natural body length (L_N), body mass, body condition, age, back-calculated smolt length, age at smoltification, and number of previous marine seasons prior to tagging of fish in the different groups.

	Tagging group				
	HS12	HA12	SA12	SS13	HS13
Tagging date	12–14 April 2012	17–18 September 2012	19–20 September 2012	22–23 April 2013	3–12 May 2013
Capture and tagging site	Søa (Lake Rovatnet)	Søa (Lake Rovatnet)	Snilldalselva (river and river mouth)	Snilldalselva (river mouth)	Søa (river mouth)
n	30	21	20	15	29
Natural length (mm)					
Mean±SD	396±61	412±121	392±75	381±53	417±55
Range	335–600	270–700	310–650	275–460	330–580
Body mass (g)					
Mean±SD	586±287	866±908	581±419	620±286	713±337
Range	330–1600	210–3660	310–2180	220–1210	300–1970
Fulton's *K*					
Mean±SD	0.90±0.12	0.95±0.12	0.89±0.09	1.05±0.10	0.89±0.10
Range	0.74–1.22	0.77–1.30	0.73–1.07	0.87–1.33	0.75–1.07
Scale reading estimates					
Smolt length (mm)					
Mean±SD	166±42	182±52	132±30	140±34	137±32
Range	105–270	112–276	98–197	102–236	96–210
n (%)	22 (73%)	14 (67%)	18 (90%)	12 (80%)	22 (76%)
Age at smoltification (years)					
Mean±SD	2.63±0.72	3.00±0.74	2.35±0.61	2.27±0.65	2.19±0.40
Range	2–4	2–4	2–4	2–4	2–3
n (%)	16 (53%)	12 (57%)	17 (85%)	11 (73%)	21 (72%)
Previous marine seasons					
Mean±SD	3.39±1.24	3.92±2.36	3.43±1.02	2.40±0.52	3.06±0.68
Range	2–7	2–10	2–6	2–3	2–4
n (%)	18 (60%)	13 (62%)	14 (70%)	10 (67%)	16 (55%)
Age (years)					
Mean±SD	5.69±1.65	6.73±2.37	5.85±1.28	4.78±0.83	5.20±0.77
Range	4–10	4–13	5–9	4–6	4–7
n (%)	13 (43%)	15 (71%)	13 (65%)	9 (60%)	15 (52%)

Receiver performance

Receivers recorded transmitter identification code (individual fish identity), detection date, and time for each signal received. Receiver range was tested at the middle receiver of array H1 (Fig. 1) on 22 August 2013 (calm, clear weather, high tide) and at the Hafsmo salmon farming site (Fig. 1) on 3 December 2013 (calm, clear weather, slack tide) by deploying a transmitter (model ADT-9-long, 146 dB re 1uPa @1 m) at 3 and 5 m depth and at increasing distance from the receiver in steps of 50 m. The maximum receiver range was on both occasions 300–350 m. The transmitter model used in the range test was expected to have the shortest range of all transmitter models used in the study, based on its technical specifications.

Scale sample analysis

A small number of fish scales (five to seven scales) were sampled from the studied animals during the tagging procedure. Information obtained from the scales on smolt length, age at smoltification, age when studied, and numbers of previous seaward migrations were used in the analyses of the migratory behaviour. Scale growth was assumed to be proportional to length growth (Dahl 1910; Lea 1910; Závorka et al. 2014). The ages assigned by the research team to the experimental animals were verified by sending a subsample of the scales for reading by personnel at the Norwegian Institute for Nature Research and the Technical University of Denmark. Uncertain values of age, length, and age at smoltification and number of previous seaward migrations were excluded from analyses.

The sea trout tagged in the river mouth of River Søa during spring 2013 (HS13) had uncertain river of origin, due to presence nearby (500 m) of another watercourse housing sea trout. This group of fish was therefore separated from the groups tagged in Lake Rovatnet when analysing morphology and life history of the individuals by the watercourses of tagging.

Data analysis

Data filtering

The initial number of detections (registrations) logged onto all receivers used in the study was 5 147 075. Mean number of detections of the tagged individuals was 44 745 (SD = 91 294, range 0–597 433). A total of 1360 (0.03%) registrations with false IDs were excluded from the dataset. Data from the two receivers in the outlet of the River Søa and the three innermost receivers in Snillfjord were anticipated to contain higher frequencies of false detections because of concurrent signals from high numbers of simultaneously occurring tagged fish. Concurrent signals (tag collisions) can confound receiver detections and generate false ID codes. A data filter that required at least two registrations from a tagged individual within a time span of 10 min was applied to these receivers, which excluded 46 223 (0.90%) registrations from further analyses.

Statistical analyses and computer software

After sorting and extracting data using Access 2013 and Excel 2013 (Microsoft Co., USA), the statistical analyses were conducted using R version 2.15.3 (www.r-project.org). For one- and two-way analysis of variance (ANOVA) between two groups, Welch's *t* tests were conducted, assuming unequal variance. For ANOVA among three or more groups, Tukey's ANOVA was conducted using the R package Multcomp (Hothorn et al. 2008).

The hypothesis that numbers of days spent at sea depended on some combination of fish age, body length, condition factor, previous number of times the fish had been to sea, time of sea entry (Julian day number), maximum distance migrated away from the home river, and smolt age and length was tested using the R package MuMIn (Bartoń 2015). In total, 576 models of varying complexity were fitted for hypothesis testing. To avoid autocorrelation between body length and condition factor, residual values (resvalbc) from the linear model log(condition) ~ log(length) were used instead of the body condition per se. The global model included age at tracking, length (L_N), resvalbc, previous number of times the fish had been to sea, time of sea entry, short-, medium-, or long-distance migratory strategy, back-calculated smolt age and smolt length, and the interaction terms length × resvalBC, strategy × length, and strategy × resvalbc. The other 575 models were all nested models from the global model. The approximating models were compared using Akaike's information criterion (AIC) (Anderson et al. 2001). AIC ranks the candidate models to determine which model provides the best description of the data with the fewest parameters. The hypothesis was tested for those 27 sea trout for which data on all variables were available.

Defining short-, medium-, and long-distance migrants

The fish were categorized as short-, medium-, or long-distance migrants according to the maximum distance at which they were detected from their release point during 1 April – 1 October in either 2012 or 2013 (see Fig. 1). Short-distance migrants were only recorded at receivers up to 4 km from the river mouth. Medium-distance migrants were registered up to 10 km from the river mouth for fish tagged in Søa watercourse and up to 13 km for the fish tagged in River Snilldalselva. Long-distance migrants were registered at receivers more than 10 km from the river mouth for fish tagged in Søa watercourse and more than 13 km for fish tagged in River Snilldalselva. The slight difference in the distances that defined migrant groups for the two watercourses (10 versus 13 km) was due to logistical concerns that resulted in different distances between the receiver arrays in the two fjords. Fish that did not return to fresh water and were not recorded by any receiver in the marine habitat after 1 July in either 2012 or 2013 were excluded from the migration distance analysis, because they potentially were lost from the study before they had reached their maximum dispersal. An exception was done for fish registered at receivers more than 10 km (Søa watercourse) or 13 km (River Snilldalselva) from the river mouths, since they already had been recorded as long-distance migrants.

Calculating marine residence time

The study area was divided into different zones based on geographic location (Fig. 1). Residence time was only calculated for individuals returning to fresh water or for fish recorded in the fjord after 1 October in 2012 or 2013. The calculation of residence time by tagged fish in different fjord zones was carried out using the following criteria:

1. In the case of a transition to a zone further out in the fjord, the residence time in the next zone started at the time of the last registration at a receiver in the previous zone.
2. In the case of transition to a zone further into the fjord, the residence time in the next zone started at the time of the first registration at a receiver in the inner zone.
3. For transitions into fresh water, the freshwater residence started at the time of the last registration at a river mouth receiver.
4. For transitions from freshwater to fjord zones, the fjord residence started at the first registration at a river mouth receiver.

Receivers in river mouths were considered as part of the fjord. For the fish tagged in 2013, estimated marine residence times were considered as minimums, since the fish were captured in the river mouths, and it was possible that they had spent a preceding period in marine habitat before they were tagged. Nine fish tagged in Lake Rovatnet in spring 2012 conducted sea migrations during summer in both 2012 and 2013. These fish were only included in the statistical analyses of marine residence during the first year to avoid repeated measures concerns.

Use of pelagic versus littoral habitats

The receiver arrays that contained both pelagic and nearshore receivers (arrays H1, H2, H3, and S1; Fig. 1) were used to investigate the importance of littoral and pelagic habitats for the tagged sea trout. Receivers deployed near the shore or in areas with shallow water (<10 m depth) where the sea trout was likely to feed at or near the bottom or along cliff walls within the receiver range were defined as nearshore receivers. Receivers deployed over deep water, without coastline or shallow areas (<25 m depth) within the receiver range, were defined as pelagic receivers. The proportional numbers of littoral and pelagic registrations at the receiver arrays, corrected for the proportion of littoral (eight receivers) versus pelagic (nine receivers), were investigated for each fish for the period 1 April – 1 October in 2012 or 2013. This was assumed to give a rough estimate of relative preference of littoral and pelagic habitats. Potential differences between littoral and pelagic habitats were tested with a χ^2 test.

Results

Environmental parameters

From 1 May to 1 October, marine water temperatures in the study area varied from 3.8 to 19.4 °C. The salinity levels during the same period were brackish in the outer areas (2012: mean ± SD = 28‰ ± 1.8‰, 2013: mean ± SD = 21‰ ± 2.0‰), the inner Hemnfjord (2012: mean ± SD = 29‰ ± 2.7 ‰, 2013: mean ± SD = 23‰ ± 7.6‰), and the inner Snillfjord (2012: mean ± SD = 26‰ ± 4.7‰, 2013: mean ± SD = 24‰ ± 4.8‰).

Morphological characteristics of tagged fish

Among the study animals, there was considerable variation both among individuals (Table 1) and tagging groups (Table 2) regarding body size, body condition, age, back-calculated smolt length, age at smoltification, and number of previous marine seasons.

The two groups of fish tagged in Lake Rovatnet (HS12 and HA12) had greater mean smolt length, higher mean age at smoltification, higher mean age, and a tendency towards having spent more previous seasons at sea than the groups of fish tagged in River Snilldalselva (SA12 and SS13; Table 2). Similarly, the groups of fish tagged in Lake Rovatnet had higher mean smolt lengths, ages at smoltification, and total age than the fish tagged in the mouth of River Søa (HS13; Table 2).

Sea trout tagged in River Snilldalselva (SA12 and SS13) had lower mean natural length and greater mean body condition than the group of fish tagged in the mouth of River Søa (HS13; Table 2). The fish tagged in the mouth of the River Snilldalselva during the spring of 2013 (SS13) had a higher body condition at tagging than the fish tagged both in Lake Rovatnet in spring 2012 (HS12,) and in the mouth of River Søa in spring 2013 (HS13; Tables 1 and 2).

Fish tagged in the River Snilldalselva during autumn 2012 (SA12) had shorter body lengths at smoltification than the fish tagged in Lake Rovatnet in spring 2012 (HS12) and autumn 2012 (HA12; Table 2). Similarly, at smoltification fish tagged in Lake Rovatnet in autumn 2012 (HA12) had greater body length than individuals tagged in the mouth of River Søa (HS13) and in the river mouth of River Snilldalselva (SS13) during spring 2013 (Table 2).

The group of fish tagged in Lake Rovatnet during autumn of 2012 (HA12) had greater ages at smoltification than those tagged in the mouth of River Søa in spring 2013 (HS13), in River Snilldalselva in autumn 2012 (SA12), and in the mouth of River Snilldalselva in spring 2013 (SS13; Table 2). The fish tagged in Lake Rovatnet in

Table 2. Differences in morphology and life history among fish from watercourses and tagging groups.

Morphological and life history characteristic	Alternative hypothesis (H_1)	Statistical test	n	P
Fish tagged in Lake Rovatnet versus fish tagged in River Snilldalselva				
Body length	HS12 and HA12 < or > SA12 and SS13	t test	86	0.321
Body condition	HS12 and HA12 < or > SA12 and SS13	t test	86	0.127
Smolt length	HS12 and HA12 ≤ SA12 and SS13	t test	66	**<0.001**
Age at smoltification	HS12 and HA12 ≤ SA12 and SS13	t test	56	**0.007**
Previous marine seasons	HS12 and HA12 ≤ SA12 and SS13	t test	55	**0.055**
Age	HS12 and HA12 ≤ SA12 and SS13	t test	50	**0.042**
Fish tagged in Lake Rovatnet versus fish tagged in mouth of River Søa				
Length	HS12 and HA12 < or > HS13	t test	80	0.422
Body condition	HS12 and HA12 < or > HS13	t test	80	0.258
Smolt length	HS12 and HA12 ≤ HS13	t test	58	**<0.001**
Age at smoltification	HS12 and HA12 ≤ HS13	t test	49	**<0.001**
Previous marine seasons	HS12 and HA12 < or > HS13	t test	47	0.136
Age	HS12 and HA12 ≤ HS13	t test	43	**0.012**
Fish tagged in River Snilldalselva versus fish tagged in mouth of River Søa				
Body length	SA12 and SS13 ≥ HS13	t test	64	**0.025**
Body condition	SA12 and SS13 ≤ HS13	t test	64	**0.014**
Smolt length	SA12 and SS13 < or > HS13	t test	52	0.817
Age at smoltification	SA12 and SS13 < or > HS13	t test	49	0.372
Previous marine seasons	SA12 and SS13 < or > HS13	t test	40	0.813
Age	SA12 and SS13 < or > HS13	t test	37	0.528
Differences among groups of tagging				
Body length	HS12 < or > HA12 < or > SA12 < or > SS13 < or > HS13	ANOVA	115	0.78
Body condition	SS13 ≤ HS12	Tukey ANOVA	45	**0.014**
Body condition	SS13 ≤ HS13	Tukey ANOVA	43	**0.009**
Smolt length	HS12 ≤ SA12	Tukey ANOVA	40	**0.05**
Smolt length	HA12 ≤ SA12	Tukey ANOVA	32	**0.004**
Smolt length	HA12 ≤ HS13	Tukey ANOVA	36	**0.008**
Smolt length	HA12 ≤ SS13	Tukey ANOVA	26	**0.044**
Age at smoltification	HA12 ≤ HS13	Tukey ANOVA	33	**0.004**
Age at smoltification	HA12 ≤ SA12	Tukey ANOVA	29	**0.049**
Age at smoltification	HA12 ≤ SS13	Tukey ANOVA	23	**0.044**
Previous marine seasons	HS12 < or > HA12 < or > SA12 < or > SS13 < or > HS13	ANOVA	71	0.098
Age	HA12 ≤ SS13	Tukey ANOVA	24	**0.032**

Note: HS12: Lake Rovatnet in spring 2012, HA12: Lake Rovatnet in autumn 2012, SA12: River Snilldalselva in autumn 2012, SS13: Mouth of River Snilldalselva in spring 2013, HS13: Mouth of River Søa in spring 2013. Significant P values are shown in bold; nonsignificant Tukey ANOVA values are excluded.

autumn 2012 (HA12) had greater total age than the fish tagged in River Snilldalselva in spring 2013 (SS13; Table 2).

Morphological characteristics of short-, medium-, and long-distance migrants

In total, 100 of the 115 tagged sea trout were recorded by the acoustic receivers in the fjord system. Individual sea trout were tracked from 6 to 624 days. Based on the previously described criteria, a total of 88 fish were categorized as either short-, medium-, or long-distance migrants (Table 3). The proportions of short-, medium-, and long-distance migrants varied among the tagging groups. The fish tagged in Lake Rovatnet in spring 2012 (HS12) consisted of 6 short- (26%), 5 medium- (22%), and 12 long-distance migrants (52%). All sea trout tagged in Lake Rovatnet in autumn 2012 (HA12) were long-distance migrants (11 individuals, 100%). The fish tagged in the river mouth of River Søa in spring 2013 (HS13) consisted of 19 short- (70%), 4 medium- (15%), and 4 long-distance migrants (15%). The sea trout tagged in River Snilldalselva in autumn 2012 (SA12) had 4 short- (31%), 2 medium- (15%), and 7 long-distance migrants (54%), while the those tagged in spring 2013 (SS13) consisted of 6 short- (43%), 5 medium- (36%), and 3 long-distance migrants (21%). The body lengths of the 15 individuals that were not recorded at any receivers did not differ significantly from the rest of the individuals (t test, n = 115, P = 0.22).

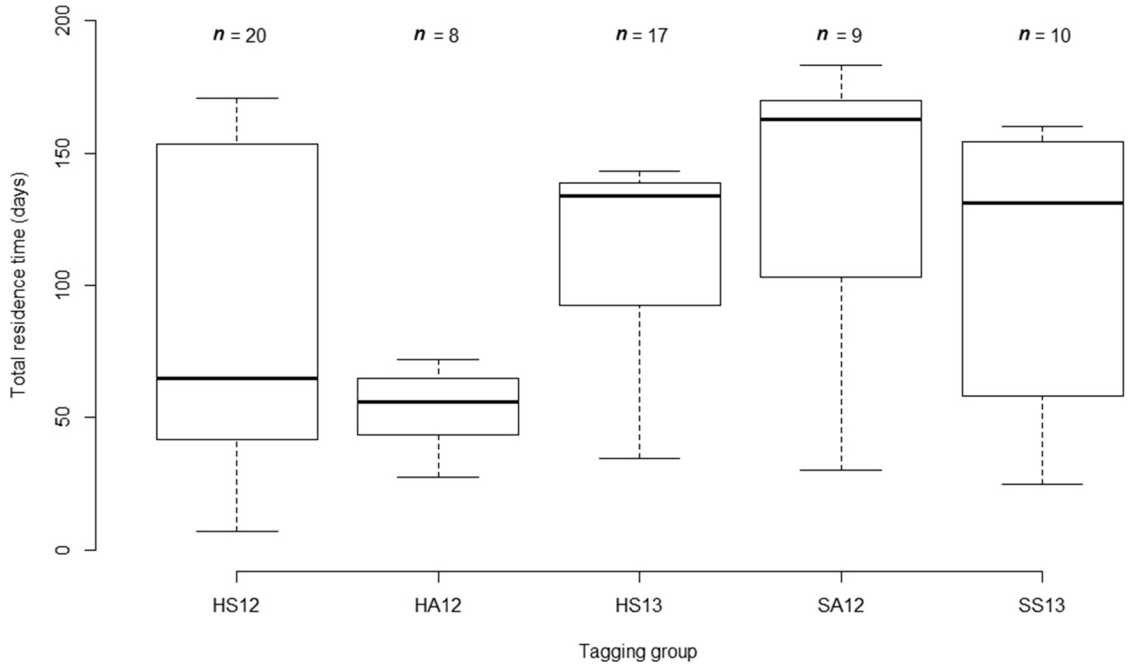
Table 3. Model selection for estimating the determinants of the duration of the marine residence time.

Model	AIC	ΔAIC	AIC weights	df
[*A*, *L*, SE, SA, *S*]	220.8160284	0	0.111953643	8
[*A*, *L*, SE, SA, SL, *S*]	221.6453596	0.829331157	0.073952227	9
[*A*, *L*, *P*, SE, SA, *S*]	222.7925525	1.976524071	0.041671725	9
[*A*, *L*, *R*, SE, SA, *S*]	222.8040131	1.987984688	0.041433616	9

Note: The models estimate the relative contributions to the duration of the marine residence time from the parameters age (*A*), body length (*L*), number of previous marine seasons (*P*), residual values (resvalbc) from the linear model log(condition) ~ log(length) (*R*), Julian day of sea entry (SE), smolt age (SA), smolt length (SL), and maximum distance migrated away from the home river (*S*). AIC is the score based on Akaike's information criterion. AIC weights represent the relative likelihood of the model. The table displays the four best-fitting of the total of 576 tested models.

There was no difference in mean L_N among short-, medium-, and long-distance migrants (Table 3; ANOVA, n = 88, P = 0.20). However, most (n = 7) of the largest individuals (≥450 mm, n = 12) conducted long-distance migrations, while fewer large individuals performed medium- (n = 3) and short-distance (n = 2) migrations. Among the smallest individuals (≤350 mm, n = 18), there were equal proportions of short- (n = 6), medium- (n = 6), and long-distance (n = 6) migrants.

Fig. 2. Total residence time (days) in the marine environment during 1 April – 1 October 2012 or 2013 for tagging groups HS12 (tagged in Lake Rovatnet in spring 2012), HA12 (tagged in Lake Rovatnet in autumn 2012), HS13 (tagged in river mouth of River Søa in spring 2013), SA12 (tagged in River Snilldalselva in autumn 2012), and SS13 (tagged in the river mouth of River Snilldalselva in spring 2013). The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes), and the 5th and 95th percentiles (whiskers).



There was large interindividual variation in mean body condition in spring (Table 3). Long-distance migrants had significantly (Tukey ANOVA) poorer body condition in spring prior to the marine migration than short- ($n = 29$, $P = 0.013$) and medium-distance migrants ($n = 33$, $P = 0.018$). The body condition in spring of short- and medium-distance migrants did not differ ($n = 44$, $P = 0.92$).

Age, back-calculated smolt length, age at smoltification and number of previous marine seasons varied among the groups of short-, medium-, and long-distance migrants (Table 3). Long-distance migrants had larger smolt lengths than both short- (Tukey ANOVA, $n = 57$, $P = 0.023$) and medium-distance migrants ($n = 43$, $P = 0.013$). The long-distance migrants had a near significant higher age at smoltification than short-distance migrants ($n = 50$, $P = 0.057$), but were similar in age to the medium-distance migrants ($n = 36$, $P = 0.104$). Long-distance migrants tended to have had more previous marine seasons than the medium-distance migrants ($n = 38$, $P = 0.057$), but not more previous marine seasons than the short-distance migrants ($n = 44$, $P = 0.255$). The long-distance migrants were older than both the short- ($n = 41$, $P = 0.043$) and the medium-distance migrants ($n = 35$, $P = 0.032$).

Among the nine fish tagged in Lake Rovatnet in spring 2012 that were followed through their sea migration both during the summer 2012 and again in 2013, there were identical numbers of short- ($n = 3$), medium- ($n = 3$), and long-distance ($n = 3$) migrants during 2012. In 2013, one short-distance migrant from 2012 performed a medium-distance migration, and one medium-distance migrant from 2012 performed a long-distance migration. The seven other individuals repeated the migration pattern from the year before. However, this change in maximum migratory dispersal was not significant, but the sample size was low (χ^2; $n = 9$, $P = 0.72$).

Marine residence time during summer

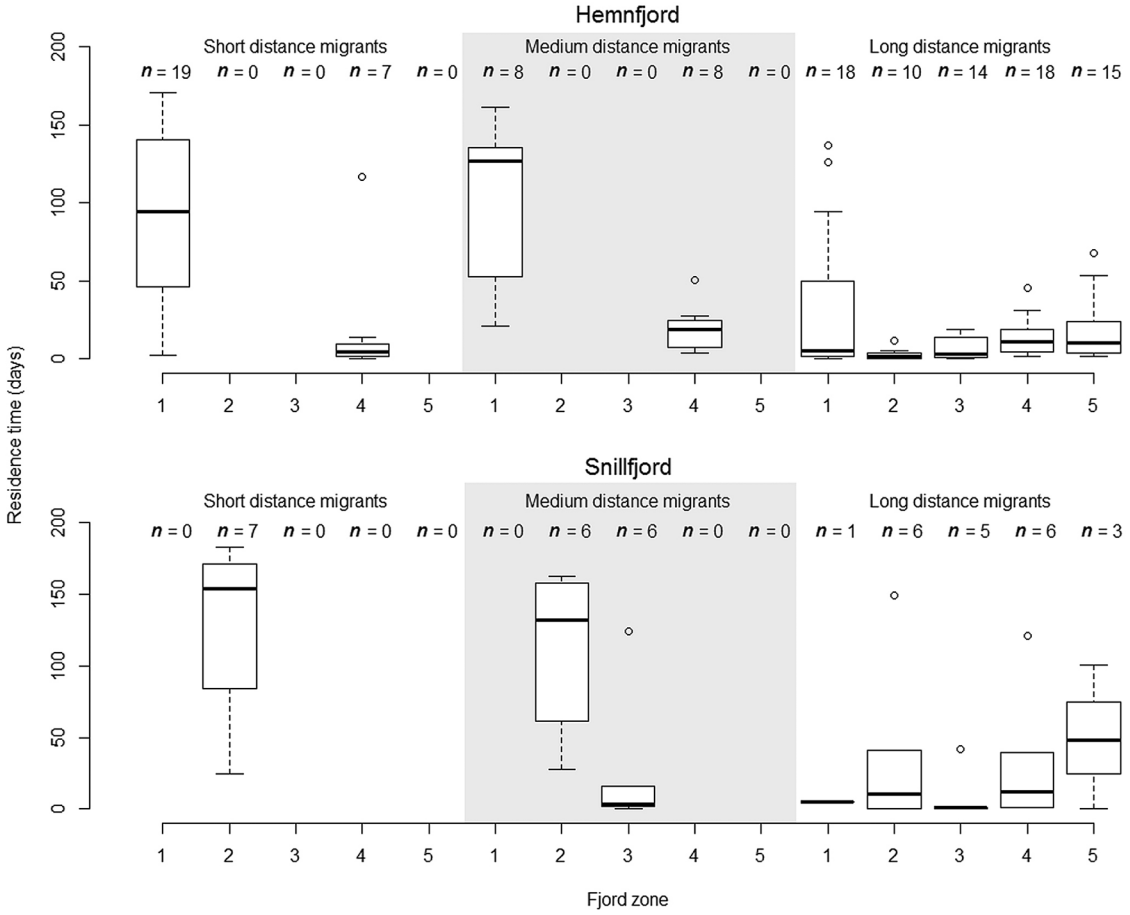
During 1 April – 1 October (2012 and 2013), 51 of the 115 tagged sea trout were never registered in the marine fjord, or else after an initial period of detections on the marine receivers, the detections stopped and the fish were not recorded returning to fresh water. The reasons for loosing track of the fish were in about half of the cases not known. However, 15 individuals were reported captured and killed by anglers, eight individuals tagged in the Lake Rovatnet were never recorded to leave the lake, and four individuals migrated out of the study area and did not return. After the study ended, two of the individuals that migrated out of the study area were recaptured by anglers 130 km southwest of their tagging location.

There was large interindividual variation in the total residence time in marine habitats during 1 April – 1 October in 2012 and 2013 (Fig. 2). Among tagged fish tracked throughout these periods, the mean marine residence time was 100 days (SD 52 days, range 7–183 days). The largest variation was found within the fish tagged in Lake Rovatnet in spring 2012 (HS12), which had a mean residence of 91 days (SD 59 days, range 7–171 days). The fish tagged in the outlet of spawning streams of Lake Rovatnet during autumn 2012 (HA12) and tracked during summer 2013 had the lowest intragroup variation with a mean marine residence time of 53 days (SD 15 days, range 27–72 days). When comparing marine residence times of the different tagging groups, the fish tagged in Lake Rovatnet in autumn 2012 (HA12) had shorter marine residence times than the fish tagged in the mouth of River Søa in spring 2013 (HS13; Tukey ANOVA, $n = 25$, $P = 0.049$) and fish tagged in River Snilldalselva in autumn 2012 (SA12; $n = 17$, $P = 0.0105$).

The four best predictive models all indicated that the number of days spent at sea was positively correlated to L_N and smolt age and negatively correlated to the Julian day number of sea entry and migration distance (Table 3). The best model ($r^2 = 0.65$, $P < 0.001$) included age, L_N, smolt age, timing of sea entry, and migration distance (Table 3).

Fish from all tagging groups utilized all areas of the fjord. However, the innermost parts of the fjord, near the tagging location of the sea trout (zones 1 and 2, up to 4 km from the river mouth) were found to be especially important areas for the tagged individuals, as they spent on average 68% (SD 39%, range 0.002%–100%) of their marine residence time in these areas (Fig. 3). Fish tagged in the Søa watercourse spent a significantly longer time in the innermost

Fig. 3. Residence time in the different fjord zones of short-, medium-, and long-distance migrants during 1 April – 1 October. The different fjord zones are indicated in Fig. 1. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes), and the 5th and 95th percentiles (whiskers). Circles indicate outliers.



part of Hemnfjord (zone 1, mean 71.1 days, SD 59.1 days, range 0.2–170.8 days) than in inner Snillfjord (zone 2, mean 0.6 days, SD 2.0 days, range 0–12.1 days; Tukey ANOVA, n = 90, P < 0.001), central Snillfjord (zone 3, mean 1.87 days, SD 4.5 days, range 0–18.7 days; n = 90, P < 0.001), central Hemnfjord (zone 4, mean 11.9 days, SD 19.9 days, range 0–116.7 days; n = 90, P < 0.001), and outer areas (zone 5, mean 6.4 days, SD 14.8 days, range 0–68.2 days; n = 90, P < 0.001). Fish tagged in the River Snilldalselva spent a longer time in the innermost part of Snillfjord (zone 2, mean 92.6 days, SD 69.1 days, range 0.002–183.0 days) than in the inner Hemnfjord (zone 1, mean 0.3 days, SD 1.1 days, range 0–5.0 days; Tukey ANOVA, n = 38, P < 0.001), central Snillfjord (zone 3, mean 10.2 days, SD 29.3 days, range 0–124.0 days; n = 38, P < 0.001), central Hemnfjord (zone 4, mean 9.9 days, SD 28.5 days, range 0–121.0 days; n = 38, P < 0.001), and outer areas (zone 5, mean 7.9 days, SD 25.1 days, range 0–101.0 days; n = 38, P < 0.001).

When comparing the residence time in the innermost parts of the fjords (zone 1 for fishes tagged in the Søa watercourse and fjord zone 2 for fishes tagged in the River Snilldalselva), there was no difference between fish tagged in the Søa watercourse and those tagged in River Snilldalselva (Fig. 3; two-sided t test, n = 64, P = 0.25). Nor were there differences between these two groups in their residence times in the central parts of Snillfjord (zone 3, n = 64, P = 0.23), central parts of Hemnfjord (zone 4, n = 64, P = 0.78), or the outer study area (zone 5, n = 64, P = 0.81).

Marine residence time versus migration distance

Long-distance migrants had, despite large interindividual variation, shorter mean marine residence time than both short- (Tukey ANOVA, n = 50, P = 0.05) and medium-distance migrants (n = 38, P = 0.005; Table 4). There was no difference between 2012 and 2013 in the mean marine residence time for long-distance migrants (two-sided t test, n = 24, P = 0.99).

Large interindividual variation in the mean residence time in the different fjord zones was observed (Fig. 3). For long-distance migrants from both Rivers Søa and Snilldalselva, the time spent in the inner fjord was significantly shorter than that for the short-distance migrants (Tukey ANOVA, Søa: n = 37, P = 0.002; Snilldalselva: n = 13, P = 0.039). Similar differences were evident between long- and medium-distance migrants from Søa (n = 26, P = 0.008) but not from Snilldalselva (n = 12, P = 0.092).

Littoral versus pelagic habitat utilization

Overall, at the receiver arrays containing both nearshore and pelagic receivers, the tagged fish had larger proportions of their registrations at receivers along the shoreline (mean 75%, SD 19%, range 37%–100%) compared with receivers in the pelagic areas (mean 25%, SD 19%, range 0%–63%; χ^2; n = 73, P < 0.001) (Fig. 4). The fish had larger proportions of registrations at receivers deployed near the shore than in pelagic areas at array H1 (nearshore: mean 76%, range 35%–100%; pelagic: mean 24%, range 0%–65%; χ^2; n = 64, P < 0.001), array S1, (nearshore: mean 80%, range 41%–100%; pelagic: mean 20%, range 0%–59%; n = 29, P < 0.001), array H2 (nearshore: mean 64%, range 0.04%–100%; pelagic: mean 36%, range 0%–96%; n = 23, P < 0.001), and at array H3 (nearshore: mean 50%, range 0%–100%; pelagic: mean 50%, range 0%–100%; n = 27, P < 0.001).

Table 4. Natural body length (L_N), Fulton's body condition, age, back-calculated smolt length, age at smoltification, number of previous marine seasons, and total marine residence time during summer of short-, medium-, and long-distance migrants.

		Short-distance migrants	Medium-distance migrants	Long-distance migrants	Total
	N (%)	35 (40%)	16 (18%)	37 (42%)	88 (100%)
Natural body length (mm)	Mean	404	380	414	404
	SD	±55	±38	±84	±67
	Range	320–580	330–460	330–690	320–690
Fulton's body condition	Mean	0.95	0.94	0.89	0.92
	SD	±0.13	±0.12	±0.11	±0.12
	Range	0.75–1.33	0.78–1.22	0.73–1.30	0.73–1.33
Scale reading estimates					
Smolt length (mm)	Mean	137	127	166	148
	SD	±35	±37	±44	±44
	n	26	12	31	69
Age at smoltification (years)	Mean	2.24	2.18	2.68	2.41
	SD	±0.52	±0.60	±0.80	±0.69
	n	25	11	25	61
Previous marine seasons	Mean	3.00	2.64	3.52	3.18
	SD	±0.61	±0.67	±1.34	±1.09
	n	17	11	27	55
Age (years)	Mean	5.13	4.90	6.12	5.57
	SD	±0.72	±0.74	±1.62	±1.35
	n	16	10	25	51
Total marine residence time (days)	Mean	108	128	76	100
	SD	±55	±41	±43	±51
	n	26	14	24	64

Long-distance migrants had higher proportions of pelagic registrations than medium-distance migrants (Fig. 5; Tukey ANOVA, $n = 146$, $P = 0.02$) and nearly significant higher portions of pelagic registrations compared with short-distance migrants ($n = 146$, $P = 0.052$; Fig. 4). Short- and medium-distance migrants did not differ in their uses of pelagic and inshore areas ($n = 146$, $P = 0.72$).

Discussion

Morphological characteristics and life history

The sea trout differed in morphology and life history both within and between the watercourses. Sea trout tagged in River Snilldalselva had better body condition than fish tagged in the Søa watercourse, and individuals tagged in the mouth of River Snilldalselva in the spring of 2013 had better body condition than the other groups of fish also tagged during the spring. Differences in body condition in the spring might be influenced by differences in overwintering conditions and whether an individual fish had spawned in the previous autumn (Jonsson and Jonsson 2011). For the fish tagged in the river mouth in the spring of 2013, their area of residence prior to tagging is not known (i.e., if they had been in the sea or fresh water). Marine residence during winter has been reported for sea trout in both the southern and northern parts of Norway (Knutsen et al. 2004; Jensen and Rikardsen 2008, 2012), and Jonsson and Jonsson (2009) found that sea trout spending the winter at sea had better growth during the first 2 years after smoltification compared with sea trout that returned to fresh water for overwintering.

Fish tagged in Lake Rovatnet did not differ in L_N or body condition from fish tagged in the River Snilldalselva, but were older and tended (nearly statistically significant) toward having experienced more previous marine seasons. Since we tagged all fish of suitable minimum sizes (>27 cm) that we captured, this may indicate a systematic difference in the ages of sea trout between the two sites. Furthermore, fish from Lake Rovatnet had a larger back-calculated mean smolt size and greater age at smoltification compared with fish tagged in the River Snilldalselva. This was probably caused by environmental differences between the watercourses. The parr in the Søa watercourse could reside in Lake Rovatnet, enabling them to have better growth before smoltification. In contrast, the River Snilldalselva offers few deep pools and there is no access to lakes. Hence, variable environmental conditions, constraints in food supply, or limited availability of appropriate shelter may cause the parr in this river to smoltify at younger age than parr in the Søa watercourse. This is consistent with previous studies on how the environment influences smoltification in partly migrating trout populations (Jonsson and Jonsson 1993; Wysujack et al. 2009). The group of fish tagged in the river mouth of River Søa in spring 2013 were smaller and younger at smoltification than the fish tagged in the Lake Rovatnet, possibly because some of these fish originated from the neighbouring watercourse.

Migratory distances

Large interindividual variation in the migration distance was observed. Some individuals remained in the innermost parts of the fjord, while others spent most of their marine residence outside the study area. The proportions of short- and long-distance migrants varied greatly among the groups of tagged fish. Fish captured at different locations and times of the year may have been at different stages in their life history, which may have influenced their subsequent migratory behaviour. Other causes for the variations observed in migratory strategies may have been due to behavioural and (or) genetic differences. Previous studies have also shown large variation in migration distance among populations of anadromous sea trout (Jensen 1968; Svärdson and Fagerström 1982; Berg and Berg 1987), which these authors attributed to combinations of environmental and genetic factors (Klemetsen et al. 2003). del Villar-Guerra et al. (2014) suggested that variables such as morphological characteristics, ontogeny, genetics, and life history might influence the sea trout's marine behaviour and the extent of its marine migration.

No difference was found in body length between short- and long-distance migrants, and individuals of all size classes performed long-distance migrations. By contrast, Jensen et al. (2014)

Fig. 4. Proportions of individuals' registrations at near shore (white) and pelagic (grey) receivers at array H1, H2, H3, and S1 during 1 April – 1 October. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes), and the 5th and 95th percentiles (whiskers). Circles indicate outliers.

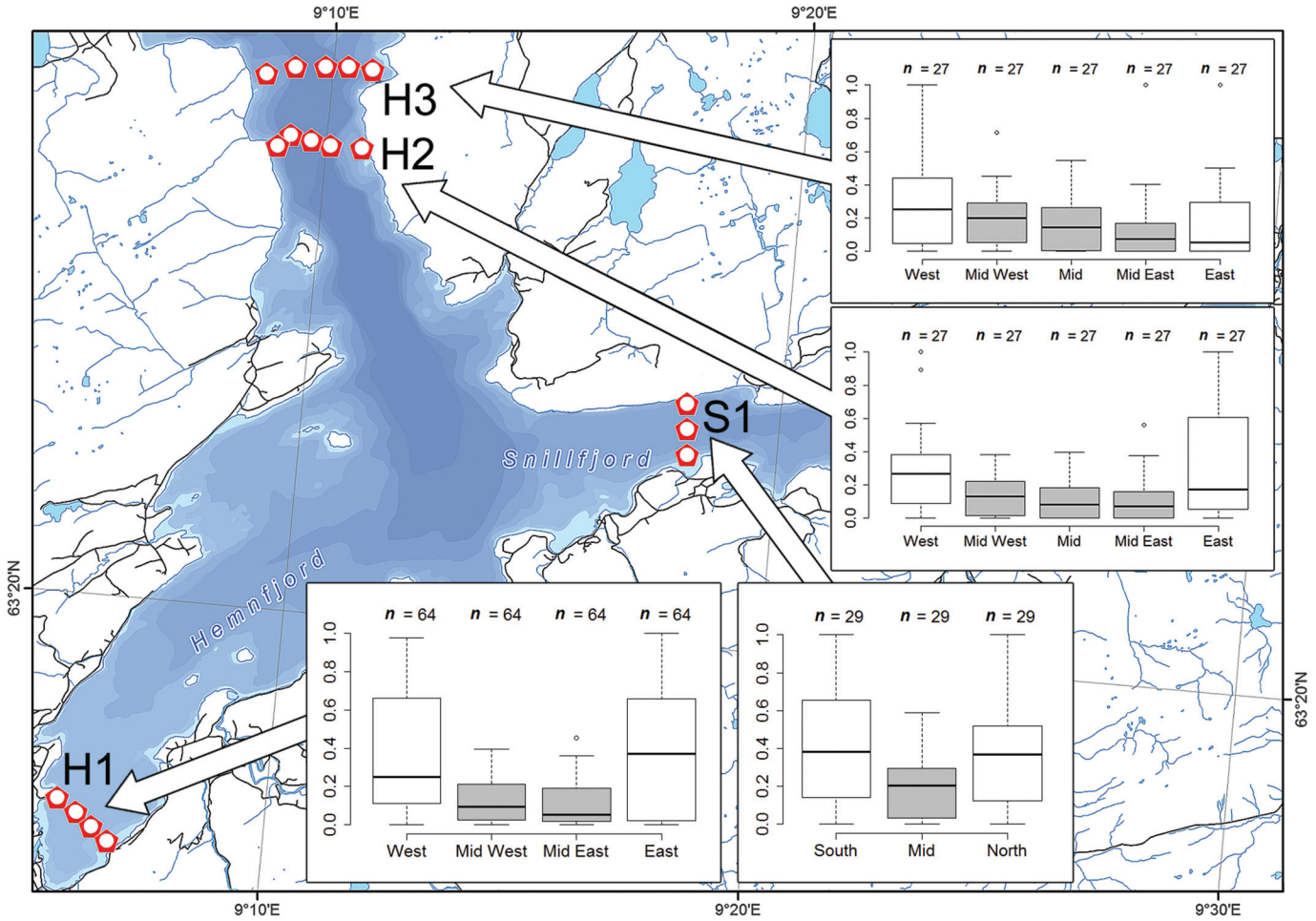
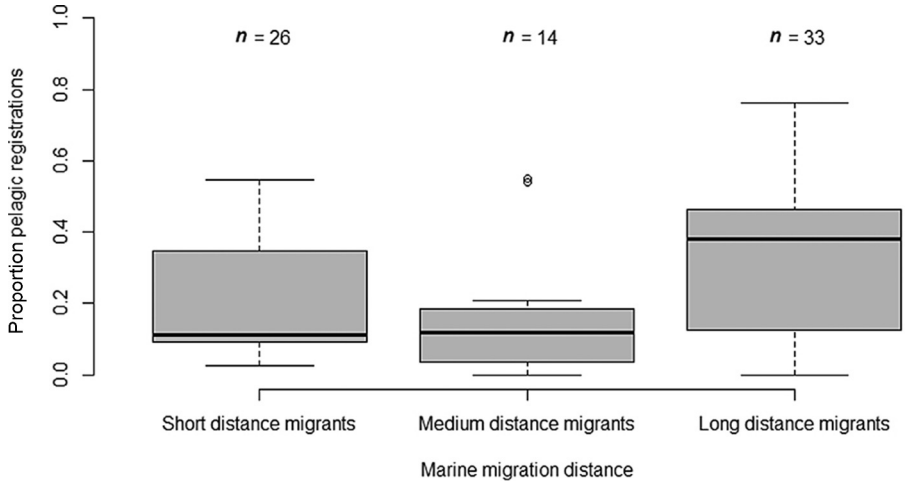


Fig. 5. Proportions of pelagic registrations at receiver arrays (H1, H2, H3, and S1) for short-, medium-, and long-distance migrants during 1 April – 1 October. The box-and-whisker plots show median values (black lines), the interquartile ranges (boxes), and the 5th and 95th percentiles (whiskers). Circles indicate outliers.



found that large individuals were more likely to conduct long-distance marine migrations than smaller individuals. They suggested that this could be caused by a higher abundance of suitable fish prey for the larger individuals further out in the fjord at their study site. Similarly, Knutsen et al. (2001) found that small postsmolt sea trout fed inshore on shallow water prey communities, while larger sea trout were feeding further offshore on pelagic fish.

Fast-growing sea trout change to a more piscivorous diet at a smaller size and younger age than slower-growing individuals (Klemetsen et al. 2003), which might explain why in this study some smaller individuals conducted long-distance migrations. Alternatively, the small long-distance migrants may have had similar feeding behaviour as the short-distance migrants, but dispersed further out in the fjord by chance or because of competition with conspecifics in inshore areas and the availability of suitable alternative habitat and conditions further away from the river mouth.

The long-distance migrants had poorer body condition than short-distance migrants at the time of tagging, suggesting that individuals with a poorer body condition experienced a greater need to maximize benefits from distant feeding opportunities. Wysujack et al. (2009) found that poor body condition promoted migratory behaviour in brown trout parr. Similarly, Davidsen et al. (2014) found that starved sea trout postsmolts migrated further out into a fjord compared with fully fed individuals. However, Boel et al. (2014) found a different pattern in their study of migration distances of brown trout in a freshwater system, where energy stores were positively correlated with migration distances. An alternative hypothesis to account for the pattern observed in this study may be that fish with poor body condition were outcompeted from the preferred shore habitats. Migratory strategies have previous been shown to be influenced by different needs for food intake (Halttunen et al. 2013), and Damsgård and Dill (1998) showed that starving fish may undertake more risky behaviour than well-fed individuals.

Marine residence during summer

Large intragroup variation in marine residence time during the summer months was observed. Individuals tagged in the Lake Rovatnet during spring 2012 had the largest intragroup variation, while individuals tagged in Lake Rovatnet in autumn 2012 had the smallest variation. Previous studies have revealed that marine residency varies both among and within populations, with a range of factors influencing the duration of the marine residence of an individual, such as age, maturity (Jonsson 1985), and environmental conditions in fresh water prior to the seawards migration (Jensen and Rikardsen 2008). In the present study, the duration of the seaward migration for 27 of the tagged fish was found to be positively correlated to L_N and smolt age, but negatively correlated to the date of sea entry.

Our fish spent on average 68% of their marine residence time in the innermost parts of the fjords, near the mouth of the river where they were tagged. Since all fish in the present study were veteran migrants with one or more previous marine seasons, and since seawater tolerance in salmonids is known to increase with body size (Hoar 1988; Ugedal et al. 1998), most individuals in the present study probably had good osmoregulatory capabilities. Larsen et al. (2008) suggested that local adaptation may cause differences in seawater tolerance among sea trout populations. However, the innermost parts of both Snillfjord and Hemnfjord had levels of salinities similar to the outer parts of the fjord system during the present study, further suggesting that salinity likely did not affect the spatial distribution of the experimental fish in the fjords to any great extent.

Long-distance migrants, who were found to be older than both short- and medium-distance migrants, surprisingly spent a shorter time at the sea than individuals moving shorter distances. Previous studies have shown that older sea trout individuals generally return earlier from the marine migration (Jonsson 1985); however, the reasons for this remain obscure.

Littoral versus pelagic habitat utilization

The sea trout stayed more often in littoral than pelagic habitats, based on the observed higher proportions of registrations of tagged fish on acoustic receivers in nearshore compared with pelagic areas. These results are consistent with findings by Jensen et al. (2014), who found that sea trout in the Alta Fjord only spent 33% of their time in the pelagic habitat. The nearshore habitat utilization is also consistent with previous studies on sea trout feeding behaviour, which suggest that the main prey (crustaceans, polychaetes, insects, and fish) are found in nearshore, shallow areas (Pemberton 1976; Knutsen et al. 2001). However, the data also show that the pelagic zone may be an important habitat for the long-distance migrants especially, and pelagic feeders are in other studies have been shown to feed almost exclusively on fish (Rikardsen and Amundsen 2005). The long-distance migrants in this study spent a minimal portion of their total marine residence time in the innermost areas of the fjord, compared with short- and medium-distance migrants. Long-distance migrants had greater proportions of pelagic registrations than medium-distance migrants and tended (nearly statistically significant) to show greater proportions of pelagic registrations compared with short-distance migrants.

Overall, the data suggests that the long-distance migrants had a higher degree of pelagic feeding behaviour, that they were in lower body condition at the start of the migration, and that they returned earlier than the medium- and short-distance migrants. It is likely that these fish found more energy-rich prey in the outer part of the fjord and therefore potentially gained mass faster and therefore also returned earlier to fresh water, as they had utilized their compensatory growth potential. Energy-rich pelagic fish species are often found to be a considerable part of the diet in larger sea trout, with herring (*Clupea harengus*) as a key prey species (Pemberton 1976; Knutsen et al. 2001; Rikardsen and Amundsen 2005; Rikardsen et al. 2006).

In summary, this study showed that sea trout both within and between watercourses draining to the same fjord system may differ in morphology, life history, migration behaviour, and marine habitat use. Such plasticity may reinforce population resilience in areas with dynamic environmental conditions or during periods of climatic changes. Altered patterns of fish migration have often been documented as an effect of contemporary global climate change (e.g., Cotton 2003; Parmesan 2007; Visser et al. 2009). A better understanding of the underlying causes of the different marine migratory strategies in sea trout is now needed to predict how changes in the marine habitat and different anthropogenic impacts may influence brown trout populations with anadromous individuals.

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